

Forest Ecology and Management 148 (2001) 135-144

Forest Ecology and Management

www.elsevier.com/locate/foreco

Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians

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Received 1 April 2000; accepted 25 May 2000

Abstract

Reptile and amphibian communities were sampled in intact gaps created by wind disturbance, salvage-logged gaps, and closed canopy mature forest (controls). Sampling was conducted during June-October in 1997 and 1998 using drift fences with pitfall and funnel traps. Basal area of live trees, shade, leaf litter coverage, and litter depth was highest in controls and lowest in salvaged gaps. Percent cover, length, and diameter of coarse woody debris (CWD) were significantly greater in intact gaps than in salvaged gaps or controls. Coarse woody debris was more decayed and had less bark in controls than gaps. The relative abundance of salamanders and American toads, and species richness and diversity of amphibians did not differ among treatments. In contrast, relative abundance of two lizard species and (marginally) snakes, and species richness and diversity of reptiles was higher in both gap treatments than in controls. Results suggest that higher light in gaps positively influenced reptile abundance, but CWD at the tested levels was not an important determinant of habitat quality. The presence of a partial canopy and other forest features in both gap treatments may have adequately retained the microclimatic conditions required by moisture-sensitive amphibians. Xeric study sites and an associated assemblage of species that are pre-adapted to relatively warm, dry conditions also might partially explain the absence of any significant response by amphibians. In the closed canopy forests of the southern Appalachians, I suggest that salamanders were historically dominant, whereas many reptile species occurred at low densities and depended upon infrequent natural disturbance to create ephemeral patches of suitable habitat. Further study is required to determine what parameters of disturbance influence reptile and amphibian communities, and how these effects might differ along a moisture gradient and among species. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Gaps; Southern Appalachian herpetofauna; Coarse woody debris; Natural disturbance and herpetofauna; Southern Appalachian reptiles; Salamanders

1. Introduction

In the predominantly closed-canopy forests southern Appalachians, natural disturbance commonly creates canopy openings at scales ranging from single-tree gaps to several hectares (Runkle, 1982; Lorimer, 1989; Greenberg and McNab, 1998). The

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gle-tree death (Runkle, 1982; Lorimer, 1989) or crown damage from ice storms. High-intensity, large-scale natural disturbance was relatively infrequent, but integral to forest dynamics at the landscape scale. Greenberg and McNab (1998) estimate that historically, 6.8% of the landscape was disturbed by high-intensity winds every 200 years. Changes in light levels to the forest floor, habitat structure, and associated changes in faunal communities are probably linked to gap size

'background' disturbance regime was historically sin-

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and canopy structure that results from partial-, single-, or multiple tree deaths.

Higher light levels promote regeneration of some tree species (Runkle, 1982; Lorimer, 1989), stimulate fruit production, and increase primary productivity that leads to higher arthropod abundance (Blake and Hoppes, 1986). Greater food resources are correlated to a higher density and diversity of birds in temperate ecosystems (Blake and Hoppes, 1986; Kilgo et al., 1999; Greenberg and Lanham, 2000). Although canopy gaps clearly function as 'hotspots' of resource availability and biological diversity within a landscape, the response of reptile and amphibian populations to canopy gaps has largely been overlooked.

Species richness of herpetofauna in the southern Appalachian mountains rivals any in the United States (Kiester, 1971; Conant and Collins, 1991). Petranka (personal communication) estimates the biomass of a streamside salamander community to be 24 times higher than bird biomass estimates from Hubbard Brook in New Hampshire (Burton and Likens, 1975a, b). Reptiles and amphibians are prey for many vertebrate predators (Pough et al., 1987). Clearly, herpetofauna are an important component of biological diversity, and also serve an important role in supporting the biological diversity of vertebrates.

Several studies in the southeastern United States suggest that timber harvesting can adversely affect local amphibian populations, especially salamanders (Blymer and McGinnes, 1977; Pough et al., 1987; Ash, 1988, 1997; Petranka et al., 1993, 1994; deMaynadier and Hunter, 1995; Phelps and Lancia, 1995). Canopy removal results in a warmer, drier microclimate, and reduced leaf litter cover and depth that could cause salamanders to desiccate (Ash, 1988; Petranka et al., 1993; deMaynadier and Hunter, 1995). Some studies report that salamanders virtually disappear from sites following clearcutting, and their populations in the southern Appalachians take at least 20 years to fully recover (Ash, 1988, 1997; Petranka et al., 1993, 1994; but see Adams et al., 1996; Harper and Guynn, 1999). deMaynadier and Hunter (1995) suggest that timber harvesting techniques that retain adequate microhabitat could mitigate impacts on many amphibian species.

The same conditions that may be detrimental to amphibians appear to benefit reptiles (Greenberg

et al., 1994; Phelps and Lancia, 1995; Adams et al., 1996). Most reptile species require warm temperatures (associated with higher light levels) for egg incubation and successful development of hatchlings (Goin and Goin, 1971; Deeming and Ferguson, 1991). However, most studies of herpetofaunal response to timber harvesting conducted in the southern Appalachians focus on a small part of the picture by addressing salamander response alone, whereas the response of reptiles has received virtually no attention.

Single- or multiple-treefalls increase light and simultaneously generate large volumes of coarse woody debris (CWD). Course woody debris has been identified as an important structural feature of habitat for optimizing terrestrial vertebrate diversity (Maser et al., 1979; Harmon et al., 1986). Many herpetofaunal species use CWD for mating sites, nesting cover (protection from desiccation and predators), feeding (CWD often attracts high densities of invertebrate prey), and thermoregulation (Whiles and Grubaugh, 1996). The presence of standing as well as down, dead CWD increases habitat structural diversity. However, little is known about how the amount, distribution, and condition of CWD influences vertebrate communities.

As the ecosystem management paradigm has gained momentum in the past decade, forest managers and ecologists have suggested that silvicultural systems be designed to mimic natural disturbance (Hansen et al., 1991; Greenberg et al., 1994). A necessary corollary is the need to identify habitat characteristics that promote diversity and abundance of species (Hansen et al., 1991; Whiles and Grubaugh, 1996). Without some knowledge of how herpetofaunal communities respond to natural disturbance and the associated changes in habitat structure, there is no way to gauge the success or failure of management.

The objective of this study was to compare the relative abundance and community composition of reptiles and amphibians in intact, wind-created downburst gaps, salvage-logged gaps, and mature, closed canopy forest. Herpetofaunal response to two levels of disturbance and associated microhabitat are examined by comparing intact gaps having relatively less light and greater cover of CWD, leaf litter, and leaf litter depth to gaps that were salvage-logged using a skidder.

2. Study area

The Bent Creek Experimental Forest (BCEF) encompasses a 2500 ha watershed in western North Carolina. Annual precipitation averages 800 mm and is evenly distributed year around. Elevation ranges from 700 to 1070 m. Winters are short and mild, and summers are long and warm. Common tree species on xeric sites such as those used in this study include scarlet oak (Quercus coccinea), chestnut oak (Q. prinus), black oak (Q. velutina), blackgum (Nyssa sylvatica), sourwood (Oxydendrum arboreum), and occasional shortleaf pines (Pinus echinata). Tulip poplar (Liriodendron tulipifera) and northern red oak (Q. rubra) dominate on moist slopes and coves. Red maple (Acer rubrum), hickory (Carya spp.), dogwood (Cornus florida) and white oak (Q. alba) are common throughout (McNab, 1996).

3. Methods

On 5 October 1995 the remnants of Hurricane Opal passed ≈ 240 km west of Asheville, NC. Downbursts of wind created at least twenty-one 0.1-1.5 ha gaps, primarily by uprooting large trees. Gaps were irregularly shaped, and retained partial canopy cover. Tree density decreased by 19–39%, and basal area (BA) by 30–52% in measured gaps (Greenberg and McNab, 1998). The uprooting of trees created pits over 1.6-4.3% of the ground surface. Several gaps were salvage-logged during 1996-1997; others were left intact, with fallen trees remaining in place.

Treatments were intact gaps (remaining as they were created by wind disturbance) (n=4), and salvagelogged gaps (n=3). Controls were mature (80-100) years old), closed canopy forest (n=4). Controls were adjacent to and >25-m from intact gaps; salvage-logged gaps were < 0.48 km from control-intact gap pairs. All study sites were < 0.4 km from streams and 0.2-2.4 km from a lake, but distances from streams or lakes were distributed relatively evenly among treatments. Salvage-logging removed standing and fallen trees that were killed or heavily damaged during hurricane Opal. One gap intended for inclusion within the salvagelogged treatment was not salvage-logged until winter 1997, and was thus included in the intact treatment that year. Hence, in 1997 $n_{\text{intact}} = 5$, $n_{\text{salvaged}} = 2$, and n_{control} =4. Study gaps ranged in size from 0.15 to 1.5 ha.

Six 7.6-m long, 0.5-m high drift fences buried 5-12 cm into the ground were established at random locations and orientations within each site. Two 19-1 plastic paint buckets with 2-mm holes drilled into the bottom for drainage were sunk flush to the ground at both ends of each fence (n=12 pitfalls per site). A sponge was placed in each bucket and dampened at each visit as necessary to reduce the probability of desiccation. Double-ended funnel traps (Heyer et al., 1994) were placed along both sides of and adjacent to each fence (n=12 per site). Pitfall and funnel traps were shaded by squares of Masonite pegboard. Erect, 1-m high PVC pipes were positioned next to each fence (n=6 per site)) during both years to attract treefrogs, and 0.6-m' treated plywood coverboards (1998 only) were placed near pitfall traps (n=12 per site) to attract herpetofauna. However, the capture success by PVC (0 captures) and coverboards (11 captures) was negligible, and those data are excluded from analyses.

Traps were open during 28 May-23 October 1997, and during 2 June 1998-29 May 1999. Traps were checked three times weekly. Reptiles and amphibians were identified, measured, weighed, and individually marked by toe- or scale-clipping, and released at point of capture.

3.2. Habitat measurements

Percent cover of habitat features including bare ground, shrub, leaf litter, humic mat, shrub, and coarse woody debris (>12.5 cm diameter at contact point with line transect) was measured in summer, 1998 using five randomly located 15-m line transects in each site. Depth of leaf litter and humic mat was measured at meters 0, 7.5, and 15 of each line transect. Length and diameter (at contact point with line transect) of each piece of CWD encountered along transects were measured. The bark condition of CWD was categorized as follows: 1, recently dead with 100% of bark on tree; 2, >70% of bark on tree; 3, 40-69% of bark on tree; 4, 10-39% of bark on tree; 5, <10% of bark on tree. Wood decay was subjectively categorized as follows: 1, no visible decay; 2, slight decay; 3, moderate decay; 4, slight fragmentation evident; 5, heavy fragmentation; 6, completely disintegrated but still distinguishable as CWD.

Percent light was determined using a spherical densiometer. Basal area of live trees and snags was calculated from diameter at breast height (DBH) measurements of all trees \geq 12.5 cm DBH, measured in fixed rectangular plots that were 0.1 ha in gaps and 0.2 ha in controls. For a detailed characterization of five intact gaps (including the four that were trapped in this study) within the study area, see Greenberg and McNab (1998).

3.3. Statistical analysis

Analysis of the full-year (2 June 1998-29 May 1999) data yielded results that were statistically similar to those using data only from June to October in both years. Therefore, I used in reported analyses only data collected during June-October in both years so that between-year data were comparative. Two-way ANOVA (SAS, 1990) was used to test for differences among treatments, years, and treatment x year interaction effects in the relative abundance of individuals within taxonomic levels including species, order, and class (if total $n \ge 30$). Two-way ANOVA was also used to test for differences in species richness and Shannon's diversity index (Brower and Zar, 1977). Although the year and interaction effects were insignificant (p>0.05) in all cases, data from both years could not be pooled for one-way ANOVA because of different between-year sample sizes for intact and salvaged gaps. Because two-way ANOVA decreases power relative to one-way ANOVA, reported results are conservative. Differences among treatments were determined using least squares means tests (SAS, 1990). Recaptured animals were excluded from data analyses. One-way ANOVA (SAS, 1990) was used to test for differences in structural habitat features among treatments. Percentage data were square-root arcsine transformed prior to statistical testing. Significance is reported at the p<0.05 level unless otherwise specified.

4. Results

4.1. Herpetofaunal response

A total of 510 amphibians (8 species) and 238 reptiles (11 species) was captured 765 times during the 1997 and 1998 trapping periods (Table 1). No

animals (with the possible exceptions of one *Sceloporus undulatus* and one *Carphophis amoenis* that moved from an intact gap to a nearby salvaged gap) were recaptured at study sites other than that of their original capture. This suggests that little movement between study sites occurred, and that study sites were therefore statistically independent. Year and treatment x year effects were insignificant (*p*>0.05) in all statistical comparisons thus only treatment effects are reported. Species richness and diversity differed significantly among treatments for reptiles but not for amphibians (Table 2).

There were no significant differences in relative abundance of total amphibians, or of caudates, anurans, or any individual species tested (Table 1). In contrast, the relative abundance of reptiles was significantly higher in both gap treatments than in controls. Both lizard species, *Eumeces fasciatus* and S. *undulatus*, were significantly more abundant in both gap treatments than in controls. No differences in relative abundance of individual snake species were detected (most species were captured too infrequently to validly test), but total snake abundance was marginally significantly greater in both gap treatments than controls (p=0.0930) (Table 1).

4.2. Habitat characteristics

Live tree BA was significantly higher in controls than in intact or salvaged gaps, and standing dead tree BA was significantly lower in salvaged gaps than other treatments (Table 3). Percent light differed significantly among all treatments, with highest light levels in salvaged gaps, and lowest in controls. Leaf litter cover was highest in controls and lowest in salvaged gaps. Litter depth was significantly lower in salvaged gaps than controls (and lower than intact gaps at p=0.0641). Percent cover of humic mat was significantly lower (p < 0.05) and depth was (marginally) significantly shallower (p=0.0905) in salvaged gaps than in intact gaps or controls. Salvaged gaps had highest and controls the least bare ground cover; bare ground in intact gaps did not significantly differ from salvaged gaps or controls (Table 3).

Percent cover of CWD was significantly higher in intact gaps than in salvaged gaps or controls (Table 4). CWD pieces were significantly longer in intact gaps than salvaged gaps or controls. Coarse woody debris

Table 1 Mean number (\pm S.E.) of amphibians and reptiles captured during June-October 1997 and 1998 using drift fences and pitfall traps in intact and salvage-logged gaps, and closed canopy mature forest controls at the Bent Creek Experimental Forest, Asheville, NC"

Species	Year	N	Treatment			MS (treat)	F (treat)	p (treat)
			Intact	Salvaged	Control			
Amphibians								
Ambystoma opacum	1997	2	0.20 ± 0.20	0.00 ± 0.00	0.25 ± 0.25	N/A	N/A	N/A
	1998	1	0.00 ± 0.00	0.00 ± 0.00	0.25 ± 0.25			
Eurycea wilderae	1997	4	0.40 ± 0.24	0.50 ± 0.50	0.25 ± 0.25	N/A	N/A	N/A
·	1998	5	0.25 ± 0.25	0.67 ± 0.33	0.50 ± 0.29			
Notophthalmus viridescens	1997	31	2.20 ± 1.50	1.00f0.00	4.50 ± 3.84	9.73	0.49	0.6201
-	1998	31	1.75 ± 1.11	3.33 ± 1.76	3.65 ± 2.25			
Plethodon oconaluftee	1997	156	13.00 ± 2.59	11.50f0.50	17.00 ± 1.08	21.58	0.53	0.5982
	1998	149	14.75 ± 5.02	11.67f3.71	13.75 ± 3.12			
Pseudotriton ruber	1997	13	0.80 ± 0.20	0.50 ± 0.50	2.00 ± 0.91	N/A	N/A	N/A
	1998	12	0.50 ± 0.50	1.00 ± 0.58	1.75 ± 0.75			
Total caudata	1997	206	16.60 ± 2.38	13.50 ± 0.50	24.00 ± 3.39	84.34	1.81	0.1950
	1998	198	17.25 f4.61	16.67 ± 4.81	19.75 ± 2.87			
Bufo americanus	1997	20	3.20 ± 0.86	0.50 ± 0.50	0.75 ± 0.48	3.68	0.14	0.8667
	1998	62	4.75 ± 2.25	4.67 ± 3.28	7.25 ± 4.70			
Ranu clamitans	1997	12	0.20f0.20	0.45 ± 0.45	0.50 ± 0.29	N/A	N/A	N/A
	1998	11	0.25 ± 0.25	2.33 ± 2.33	0.75 ± 0.48			
Rana sylvatica	1997	0	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	N/A	N/A	N/A
1107700 0,5-1-1-1	1998	1	0.00 ± 0.00	0.00 ± 0.00	0.25 ± 0.25			
Total anura	1997	32	3.40f0.81	5.00 ± 4.00	1.25 ± 0.25	5.07	0.19	0.8310
10111	1998	74	5.00f2.16	7.00 ± 3.51	8.25 ± 4.63	0.0.	0.10	0.0010
Total amphibians	1997	238	20.00 ± 1.92	18.50 ± 3.50	25.25 ± 3.35	76.78	1.61	0.2313
	1998	272	22.25 ± 3.50	23.67 ± 6.49	28.00f3.32			
Reptiles								
Agkistrodon contortix	1997	0	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	N/A	N/A	N/A
8	1998	1	0.25 ± 0.25	0.00 ± 0.00	0.00 ± 0.00			
Carphophis amoenis	1997	35	3.80 ± 2.24	7.00 ± 6.00	0.50 ± 0.29	36.79	1.93	0.1770
	1998	21	4.00 ± 3.08	1.67 ± 1.67	0.00 ± 0.00			
Coluber constrictor	1997	3	0.20 ± 0.20	0.50 ± 0.50	0.25 ± 0.25	N/A	N/A	N/A
	1998	0	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1471	1 11 1	
Diadophis punctatus	1997	27	3.20 ± 1.07	3.00 ± 1.00	1.25 ± 0.95	3.84	1.28	0.3048
	1998	10	1.50 ± 0.87	0.33 ± 0.33	0.75 ± 0.48			
Elaphe obsoleta	1997	2	0.20 ± 0.20	0.50 ± 0.50	0.00 ± 0.00	N/A	N/A	N/A
	1998	0	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	N/A	N/A	N/A
Storeria occipitomaculata	1997	1	0.20 ± 0.20	0.00 ± 0.00	0.00 ± 0.00	N/A	N/A	N/A
Storeria Coorpitomacurata	1998	5	0.75 ± 0.75	0.67 ± 0.33	0.00 ± 0.00			
Thamnophis sirtalis	1997	1	0.20 ± 0.20	0.00 ± 0.00	0.00 ± 0.00	N/A	N/A	N/A
Thumhophis siftails	1998	2	0.00 ± 0.00	0.33 ± 0.33	0.25 ± 0.25		11/11	
Total serpentes	1997	69	$7.80 \pm 2.44 \text{ a}^{\text{b}}$	1.00 ± 7.00 a	2.00 ± 0.20 2.00 ± 1.41 b	79 13	2.77	0.0930
Total scipences	1998	39	6.50 ± 3.93	3.00 ± 2.08	1.00 ± 0.71	70.10	2.11	0.0000
Lacertilia								
Eumeces fasciatus	1997	43	4.80f0.97 a	7.00 ± 1.00 a	1.25 ± 1.25 b	28.31	7.16	0.0060
	1998	32	$4.00\pm0.71\mathrm{a}$	$3.33 \pm 1.45 \text{ a}$	1.50f0.65 b		7.10	0.0000
Sceloporus undulatus	1997	23	3.00f0.84 a				4.46	0.0288
occioporas mananas		2 3 2 7	4.50 ± 2.22	2.33 ± 0.33	$0.2510.25$ b 0.50 ± 0.50	£3.00	7.70	0.0200
Total lacertilia	1998		7.80 ± 2.22 7.80 ± 1.59 a	2.53 ± 0.53 10.50 ± 1.50 a	0.50 ± 0.50 1.50 ± 1.50 b	102.66	9.90	0.0016
Total lacertilia	1997	6 6 5 0		5.67 ± 1.20 a		102.00	5.50	0.0010
Chaladan ann 11	1998	59	8.50 ± 2.33 a		2.00 f0.91 b	NI/A	NT/A	NT / A
Chelydra serpentina	1997	3	0.00 ± 0.00	1.50 ± 1.50	0.00 ± 0.00	N/A	N/A	N/A
	1998	0	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00			

Table 1 (Continued)

Species	1	Year	N	Treatment	Treatment			F (treat)	p (treat)
				Intact	Salvaged	Control			
Terrap	ene carolina	1997	2	0.20 ± 0.20	0.50 ± 0.50	0.00 ± 0.00	N/A	N/A	N/A
•		1998	0	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00			
Total	testudines	1997	5	0.20 ± 0.20	2.00 ± 2.00	0.00 ± 0.00	N/A	N/A	N/A
		1998	0	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00			
Total	reptiles	1997	140	15.80 ± 2.96 a	$23.50 \pm 7.50 \text{ a}$	$3.50 \pm 2.87 b$	388.26	10.69	0.0011
	•	1998	98	15.00 ± 3.67 a	8.67 ± 1.20 a	3.00 ± 1.41 b			

^a Statistical results are for two-way ANOVA using treatment (df=2), year (df=1), and treatmentxyear (df=2) as factors. Year and treatmentxyear effects were insignificant (p>0.05) for all tests and are not included in reported results.

Table 2
Mean (±S.E.) species richness and Shannon's diversity index (*H'*) of reptiles and amphibians captured during June-October 1997 and 1998 using drift fences and pitfall traps in intact and salvage-logged gaps, and closed canopy mature forest (controls) at the Bent Creek Experimental Forest, Asheville, NC"

Species	Year	Treatment		MS (treat)	F (treat)	_P (treat)	
		Intact	Salvaged	Control			
Amphibians							
Richness	1997	4.2 ± 0.4	4.0 ± 1.0	4.0 ± 0.7	0.936	0.76	0.4854
	1998	3.5 ± 0.3	4.0 ± 0.6	5.0f0.7			
Diversity (H')	1997	0.41 ± 0.03	0.40 ± 0.03	0.33 ± 0.09	0.003	0.22	0.8053
	1998	0.36 ± 0.07	0.46 ± 0.05	0.47 ± 0.08			
Reptiles							
Richness	1997	$4.4 \pm 0.4 a^{b}$	$6.0 \pm 1.0 a$	$1.8 \pm 1.2 \text{ b}$	17.12	7.14	0.0061
	1998	$3.5 \pm 0.6 a$	$3.7 \pm 0.9 \text{ a}$	$1.8 \pm 0.8 \text{ b}$			
Diversity (H')	1997	$0.55 \pm 0.04 a$	0.63 ± 0.04 a	0.23 f0.14 b	0.27	6.27	0.0097
	1998	$0.43 \pm 0.08 \text{ a}$	0.47f0.11 a	0.15 10.15 b			

^a Statistical results are for two-way ANOVA using treatment (df=2), year (df=1), and treatmentxyear interaction (df=2) as factors. Neither year nor treatmentxyear interaction were significant factors (p>0.10) for either index, and are thus omitted.

Table 3

Percent cover (\pm S.E.) of select microhabitat features in intact (n=4) and salvage-logged (n=3) gaps created in 1995 by hurricane Opal, and closed canopy, mature forest (controls) (n=4)^a

Feature Treatment				M S	F-value	p-Value
	Intact	Salvaged	Control			
Bare ground (%)	$1.5 \pm 0.6 \text{ a,b}^{\text{b}}$	5.6 ± 2.4 b	0.5 ± 0.3 a	89.75	6.26	0.0230
Shrub (%)	$55.6 \pm 7.3 \text{ a}$	$29.3 \pm 8.0 \text{ b}$	$26.6 \pm 6.6 \text{ b}$	371.6	4.67	0.0450
Leaf litter (%)	$89.5 \pm 2.5 a$	$76.4 \pm 2.7 \text{ b}$	99.1 f 0.2 c	492.1	37.04	< 0.0001
Leaf litter depth (cm)	$3.4 \pm 0.6 \text{ a,b}$	1.6 ± 0.1 a	2.8f0.1 b	0.0003	4.89	0.0411
Humic mat (%)	$80.2 \pm 9.4 \text{ a}$	19.7 ± 19.7 b	$98.8 \pm 0.7 \text{ a}$	4191.0	13.74	0.0030
Humic mat depth (cm)	1.8f0.4	0.3 ± 0.3	2.0 ± 0.6	0.0003	3.29	0.0905
Light (%)	$29.1 \pm 2.3 \text{ a}$	$50.4 \pm 3.3 \text{ b}$	$3.3 \pm 0.5 \text{ c}$	1110.1	160.2	0.0001
Live tree BA (m ² /ha)	$9.8 \pm 1.6 \ a$	$9.0 \pm 1.0 \text{ a}$	$27.8 \pm 1.9 \text{ b}$	426.9	41.55	0.0001
Snag BA (m²/ha)	$3.2\pm0.3~a$	$0.6 \pm 0.5 \text{ b}$	$2.6\pm0.8~a$	6.0	4.82	0.0423

^a Percentages are presented as actual means, but data were square-root arcsine transformed for ANOVA.

^b Different letters within rows (reported only in the top row of each species indicate significant differences in relative abundance among treatments.

^b Different letters within rows (reported only in the top row of each species indicate significant differences in relative abundance among treatments.

b Different letters within rows denote significant differences among treatments.

Table 4
Mean percent cover (\pm S.E.) and characteristics of coarse woody debris (CWD) (>12.5 cm diameter) in intact (n=4) and salvage-logged (n=3) gaps created in 1995 by hurricane Opal, and closed canopy, mature forest (controls) (n=4)^a

Feature	Treatment			M S	F-value	p-Value
	Intact	Salvaged	Control			
CWD (%)	$2.5 \pm 0.4 a^{b}$	0.7 ± 0.4 b	0.4 ± 0.1 b	37.7	9.88	0.0070
Length (m)	$15.1 \pm 1.2 a$	$4.5 \pm 0.5 b$	$6.8 \pm 1.2 \text{ b}$	111.5	27.48	0.0005
Diameter (cm)	27.4 ± 3.8	16.8 ± 1.1	19.9 ± 2.2	16.6	3.56	0.0859
Bark class (1-5)	$2.2 \pm 0.3 \text{ a}$	$2.7 \pm 0.7 \text{ a}$	$5.0 \pm 0.0 \text{ b}$	7.4	12.81	0.0046
Wood class (1-6)	1.3 ± 0.3 a	3.5 f 0.5 b	5.3 ± 0.3 c	14.5	37.32	0.0002

^a Percentages are presented as actual means, but were square-root arcsine transformed for ANOVA.

diameter was marginally significantly higher (p=0.0859) in intact gaps relative to salvaged gaps or controls. Coarse woody debris within control sites had significantly less bark (<10%, on average) than in intact or intact gaps. CWD wood decay also was significantly lower in intact gaps than in salvaged gaps, and highest in controls (Table 4).

5. Discussion

Conditions of higher light and associated microclimate and microhabitat in both intact and salvagelogged gaps did not adversely affect amphibians, but increased reptile abundance, richness, and diversity relative to controls. Reported negative effects of clearcutting (complete removal of timber from 10 to 12 ha stands) on salamander populations are attributed to salamander desiccation in response to increased light and soil-surface temperatures, and lower humidity following complete canopy removal (Adams et al., 1996; Harpole and Haas, 1999). Other studies indicate that salamanders are resilient to less severe methods of timber removal, such as 2-age harvests (Adams et al., 1996), selection harvests (Messere and Ducey, 1998). harvesting firewood (Pough et al., 1987), thinnings, and heavy browsing by deer (Brooks, 1999). Harper and Guynn (1999) reported higher densities of southern Appalachian salamanders in moist sites (north and east-facing slopes) than dry (south and west-facing slopes), but found no correlation between salamander density and leaf-litter depth, litter weight, or canopy coverage. The partial canopy removal and high proportion of shade, leaf litter and other microclimatemodifying habitat features that remained in both gap treatments differ substantially from conditions in clearcut harvests and more closely resemble selection harvests or thinnings.

Ash (1988) reported that salamander declines were not complete until 2-3 years post-clearcut harvesting. An absence of treatment or year response by salamanders up to 3 years post-disturbance suggests that this study was of sufficient duration to detect a salamander response to disturbance if it were to occur.

Microclimatic and microsite variables in gaps are confounded, making it difficult to determine what features drive the numerical response of reptiles and amphibians. Treefalls generate CWD, but also increase light levels that subsequently lead to changes in vegetative structure and microclimate. Coarse woody debris did not appear to be a major determinant of habitat quality for reptiles or amphibians at the tested levels. Whereas percent CWD cover did not significantly differ between salvage-logged gaps and mature forest, the abundances of *E. fasciatus*, *S. undulatus*, and snakes did. Coarse woody debris cover was significantly higher in intact than salvaged gaps, but abundance of both lizard species and snakes not differ between the two gap treatments.

Despite a difference in mean light level (29 vs. 50%) between intact and salvage-logged gaps, no significant difference in numbers of reptiles or amphibians was detected. However, significantly fewer snakes and lizards (both species) were captured in mature forest that had less light (mean 3%) than both gap treatments. Further study is required to determine the disturbance parameters (least to greatest canopy removal and associated microclimate and

^b Different letters within rows denote significant differences among treatments.

microhabitat features) necessary to change the local abundance of reptiles and amphibians in the southern Appalachians.

Discrepancies among studies in amphibian response to timber harvesting could be partially due to differences in species composition that vary geographically and along moisture gradients (and hence among studies). For example, the xeric sites used in the current study limited the suite of species to those that already may be tolerant of warm, dry upland conditions. All of the commonly captured amphibians in this study, Plethodon oconaluftee (within the *P. glutinosus* complex), *Notophthalmus* viridescens efts, and B. americanus were equally abundant in both gap treatments and mature forest. Results of other studies also indicate that P. glutinosus (Barbour, 1971; Pais et al., 1988; Petranka et al., 1993, 1994), N. viridescens efts, and B. americanus (Pais et al., 1988) are tolerant of a wide range of site conditions. The severity of change to microclimate and microhabitat also may vary along moisture gradients; moist sites may experience more dramatic changes in soil or litter moisture following canopy removal than xeric sites.

Virtually all studies of herpetofaunal response to timber harvesting in the southern Appalachians focus only on salamanders (Blymer and McGinnes, 1977; Ash, 1988, 1997; Petranka et al., 1993, 1994; Phelps and Lancia, 1995), whereas reptile response has been largely overlooked. Adams et al. (1996) found that the relative abundance of reptiles increased following clearcut and 2-age harvests. Studies in fire-adapted ecosystems of the southeast indicate that many reptile species (excluding, for example, arboreal and CWD-dependant lizards) are more abundant in recently disturbed areas with open canopies, abundant light, and high availability of bare ground (Mushinsky, 1985; Greenberg et al., 1994). Many species of amphibians in these ecosystems also use the xeric uplands, but their distribution may be limited by distance to breeding ponds (Semlitsch and Bodie, 1998). In contrast, reptiles are scarce relative to terrestrial salamanders in the closed canopy forests of the southern Appalachian mountains where forest floor density estimates of single species (not total) range from 0.18 (Ash, 1988) to 2.2 (Jaeger, 1980) per m² (see Petranka et al., 1993).

In the predominantly closed-canopy hardwood forests of the southern Appalachians, terrestrial salamanders are clearly dominant at a landscape scale. Historically (and today), single-tree death and natural disturbances commonly created canopy gaps across a wide gradient of size and canopy structure. I suggest that historically, many species of southern Appalachian reptiles occurred at low densities in closed canopy forest, and were dependant upon such natural disturbances to create ephemeral patches of suitable habitat.

6. Conclusions

Conditions within both intact and salvage-logged gaps created by wind disturbance did not affect the relative abundance of amphibians when compared to closed canopy mature forest, but the relative abundance of two lizard species and snakes was higher in both gap treatments. Higher light levels and associated microclimate appeared to influence reptile abundance but CWD did not at the levels tested.

Today, both natural and anthropogenic disturbance by timber harvesting may influence the relative abundance of reptiles and amphibians at a local scale. Clearly, more research is necessary to determine how disturbance, both of natural and anthropogenic origin, impacts amphibian and reptile populations at the landscape level, and whether the effect is amplified by the co-occurrence of both. Special attention should be given to how disturbance effects are modified by landscape position given the differences in herpetofaunal communities that occur along moisture gradients, and the severity of changes that ensue following disturbance along that gradient. Finally, greater attention should be given the level of disturbance that affects significant change to herpetofaunal communities. How much canopy removal, CWD generation or removal, loss of leaf litter cover and depth, and other features of microhabitat and microclimate that change following disturbance is necessary to affect population change, and what species will be most impacted? Informed forest management decisions can be made only with a more refined understanding of how disturbance impacts herpetofaunal populations and communities at local and landscape scales.

Acknowledgements

I thank the USDA Southern Research Station and the Bent Creek Experimental Forest for supporting this project. Lindsay Smith, Becky Reidmiller, and Scott Freeman provided excellent field assistance. Virginia Gibbs, Julia Murphy, and Tracy Roof assisted in drift fence installation. Jim Petranka provided identification validation of some specimens. I also thank Jim Petranka and David Guynn for reviewing an earlier version of this manuscript.

References

- Adams, J.P., Lacki, M.J., Baker, M.D., 1996. Response of herpetofauna to silvicultural prescriptions in the Daniel Boone National Forest, Kentucky. Proc. Ann. Conf. Southeast. Ass. Fish Wildl. Ag. 50, 312–320.
- Ash, A.N., 1988. Disappearance of salamanders from clearcut plots. J. Elisha Mitchell Sci. Soc. 104, 116–122.
- Ash, A., 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. Conserv. Biol. 11, 983-989.
- Barbonr, R.W., 1971. Amphibians and reptiles of Kentucky. Univ. Ky. Press, Lexington.
- Blake, J.G., Hoppes, W.G., 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. Auk 103, 328–340.
- Blymer, M.J., McGinnes, B.S., 1977. Observations on possible detrimental effects of clearcutting on terrestrial amphibians. Bull. Md. Herp. Soc. 13, 79-83.
- Brooks, R.T., 1999. Residual effects of thinning and high white-tailed deer densities on northern redback salamanders in southern New England oak forests. J. Wildl. Manage. 63, 1172-1 180.
- Brower, J.E., Zar, J.H., 1977. Field and laboratory methods for general ecology. W.C. Brown, Dubuque, IA.
- Burton, T.M., Likens, G.E., 1975a. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest New Hampshire. Ecology 56, 1068–1080.
- Burton, T.M., Likens, G.E., 1975b. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire, Copeia, 541-546.
- Conant, R., Collins, J.G., 1991. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin Co., Boston.
- Deeming, D.C., Ferguson, M.W.J., 1991. Physiological effects of incubation temperature on embryonic development in reptiles and birds. In: Deeming, D.C., Ferguson, M.W.J. (Eds.), Egg Incubation: its Effects on Embryonic Development in Birds and Reptiles. Cambridge University Press, New York, pp. 32-37.
- deMaynadier, P.G., Hunter Jr., M.L., 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environ. Rev. 3, 230–261.

- Goin, C.J., Goin, O.B., 1971. Introduction to Herpetology. W.H. Freeman and Company, San Francisco.
- Greenberg, C.H., Lanham, J.D., 2000. In Review. Relationships between hurricane-created gaps and breeding birds in a southern Appalachian forest. Wilson Bull., submitted for publication.
- Greenberg, C.H., Neary, D.G., Harris, L.D., 1994. Effect of highintensity wildfire and silvicultural treatments on reptile communities in sand pine scrub. Conserv. Biol. 8, 1047–1057.
- Greenberg, C.H., McNab, W.H., 1998. Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. For. Ecol. Manage. 104, 170–191.
- Hansen, A.J., Spies, T.A., Swanson, F.J., Ohmann, J.L., 1991.
 Conserving biodiversity in managed forests: lessons from natural forests. BioSci. 41, 382-392.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, S., Gregory,
 S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G.,
 Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., Cummins,
 K.W., 1986. Ecology of coarse woody debris in temperate
 ecosystems. In: MacFadyen, A., Ford, E.D. (Eds.), Advances in
 Ecological Research, Vol. 15. Academic Press, New York,
 pp. 133–302.
- Harper, C.A., Guynn Jr., D.C., 1999. Factors affecting salamander density and distribution within four forest types in the southern Appalachian mountains. For. Ecol. Manage. 114, 245-252.
- Harpole, D.N., Haas, C.A., 1999. Effects of seven silvicultural treatments on terrestrial salamanders. For. Ecol. Manage. 114, 349-356.
- Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.C., Foster, M.S., 1994. Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, DC, 364 pp.
- Jaeger, R.G., 1980. Microhabitats of a terrestrial forest salamander. Copeia, 265-268.
- Kiester, A.R., 1971. Species density of North American amphibians and reptiles. Syst. Zool. 20, 127-137.
- Kilgo, J.C., Miller, K.V., Smith, W.P., 1999. Effects of groupselection timber harvest in bottomland hardwoods on fall migrant birds. J. Field Omith. 70, 404-413.
- Lorimer, C.G., 1989. Relative effects of small and large disturbances on temperate hardwood forest structure. Ecology 70. 565-567.
- Maser, C., Anderson, R.G., Cromack, K., Jr., Williams, J.T., Martin, R.E., 1979. Dead and downed woody material. In: Thomas, J.W. (Ed.), Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington. Agri. Handb. (USDA, Sci. Educ. Adm.) 553, pp. 78-96.
- McNab, W.H., 1996. Classification of local- and landscape-scale ecological types in the southern Appalachian Mountains. Environ. Mon. Assess. 39, 215-229.
- Messere, M., Ducey, P., 1998. Forest floor distribution of northern redback salamanders, *Plethodon cinereus*, in relation to canopy gaps: first year following selective logging. For. Ecol. Manage. 107, 319-324.
- Mushinsky, H.R., 1985. Fire and the Florida sandhill herpetofaunal community: with special attention to responses of *Cnemido-phorus sexlineatus*. Herpetologica 41, 333-342.

- Pais, R.C., Bonney, S.A., McComb, W.C., 1988. Herpetofaunal species richness and habitat associations in an eastern Kentucky forest. Proc. Ann. Conf. SE Ass. Fish Wildl. Ag. 42, 448–455.
- Petrauka, J.W., Eldridge, M.E., Haley, K.E., 1993. Effects of timber harvesting on southern Appalachian salamanders. Conserv. Biol. 7, 363–370.
- Petranka, J.W., Brannon, M.P., Hopey, M.E., Smith, C.K., 1994.
 Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. For. Ecol. Manage. 67, 135-147.
- Phelps, J.P., Lancia, R.A., 1995. Effects of a clearcut on the herpetofauna of a South Carolina bottomland swamp. Brimleyana 22, 3 1–45.

- Pough, F.H., Smith, E.M., Rhodes, D.H., Collazo, A., 1987. The abundance of salamanders in forest stands with different histories of disturbance. For. Ecol. Manage. 20, 1-9.
- Runkle, J.R., 1982. Patterns of disturbance in some old growth mesic forests of eastern North America. Ecology 63, 1533-1.546.
- SAS, 1990. SAS Institute, Inc., SAS Procedures Guide, Version 6, 3rd Edition, Cary, North Carolina.
- Semlitsch, R.D., Bodie, J.R., 1998. Are small, isolated wetlands expendable? Conserv. Biol. 12, 1129-1 133.
- Whiles, M.R., Grubaugh, J.W., 1996. Importance of coarse woody debris to southern forest herpetofauna. In: McMinn, J.W., Crossley, D.A., Jr. (Eds.), Biodiversity and Coarse Woody Debris in Southem Forests. Proc. Work. Coarse Woody Debris in S. For: Effects on Biodiversity. US. For. Serv. Gen. Tech. Rep. SE-94, pp, 94–100.